

THE EFFECTS OF VEGETATIVE TYPE, EDGES, FIRE HISTORY, RAINFALL AND MANAGEMENT IN FIRE-MAINTAINED ECOSYSTEMS

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ABSTRACT

The combined effects of repeated fires, climate, and landscape features (e.g., edges) need greater focus in fire ecology studies, which usually emphasize characteristics of the most recent fire and not fire history. Florida scrub-jays are an imperiled, territorial species that prefer medium (1.2-1.7 m) shrub heights. We measured short, medium, and tall habitat quality states annually within 10 ha grid cells that represented potential territories because frequent fires and vegetative recovery cause annual variation in habitat quality. We used multistate models and model selection to test competing hypotheses about how transition probabilities between states varied annually as functions of environmental covariates. Covariates included vegetative type, edges, precipitation, openings (gaps between shrubs), mechanical cutting, and fire characteristics. Fire characteristics not only included an annual presence/absence of fire covariate, but also fire history covariates: time since the previous fire, the maximum fire-free interval, and the number of repeated fires. Statistical models with support included many covariates for each transition probability, often including fire history, interactions and nonlinear relationships. Tall territories resulted from 28 years of fire suppression and habitat fragmentation that reduced the spread of fires across landscapes. Despite 35 years of habitat restoration and prescribed fires, half the territories remained tall suggesting a regime shift to a less desirable habitat condition. Measuring territory quality states and environmental covariates each year combined with multistate modeling provided a useful empirical approach to quantify the effects of repeated fire in combinations with environmental variables on transition probabilities that drive management strategies and ecosystem change.

INTRODUCTION

Lightning-caused fire regimes are major evolutionary drivers on nearly all continents (Tucker and Cadotte 2013); however, humans have greatly altered such fire regimes; degrading natural systems and ecosystem functions (Driscoll et al. 2010). Factors that influence the spatial variation in transitory dynamics of fire-maintained ecosystems are important to understand and manage to conserve biological diversity (Nimmo et al. 2013). Most fire studies focus on species or ecosystem responses relative to patterns of the last fire, but new approaches are needed to quantify landscape variation that results from repeated fires that do not burn all areas equally (Bradstock et al. 2005; Driscoll et al. 2010), especially given that a rapidly changing climate will impact disturbance regimes (Turner 2010).

The significance and management needs of biodiversity hotspots at least once maintained by natural fire are underestimated (Parr et al. 2014; Noss et al. 2015; Rundel et al. 2016). The North American Coastal plain is one such global biodiversity hotspot that needs practical models to guide science-based fire management to restore and maintain ecological conditions (Noss et al. 2015). For example, the Florida scrub-jay (*Aphelocoma coerulescens*) is a management priority that continues to decline because of habitat loss, fragmentation, and fires that are too infrequent (Breininger et al. 2014b). Florida scrub-jays inhabit the oak scrub and flatwood ecosystem, which requires prescribed fire management to sustain biodiversity and prevent catastrophic wildfires from impacting human interests because human landcover types (e.g., roads, cities) impede the spread of natural fires allowing fuels (e.g., tall shrubs, trees) to accumulate (Duncan and Schmalzer 2004). The history of disturbance patterns in oak scrub and flatwoods is relevant because disturbances influence fuels characteristics (e.g., produce dead fuels above ground) and dominant plants sprout from biomass stored underground (Menges and Hawkes 1998).

Mechanical cutting is often needed to restore oak scrub unburned for long periods because the vegetation becomes difficult to ignite and support fire spread (Schmalzer and Boyle 1998).

The numbers of repeated fires and interactions with other environmental variables (e.g., drought) have many effects on species composition and habitat structure (Zedler et al. 1983; Artman et al. 2001; Drewa et al. 2002). Relationships are often complicated by memory or legacy effects (e.g., cavities, snags, stored underground biomass) that are influenced by average, minimum, or maximum intervals between fires (Ripplinger et al. 2015; Johnstone et al. 2016). Fire history and climatic variables (e.g., droughts) interact to influence fire intensity and vegetation recovery (Clarke et al. 2014). These relationships can be nonlinear, which causes management thresholds in ecosystem state changes that are often described by resilience theory (Ghermandi et al. 2010; Mori 2011; Johnson et al. 2013). Resilience theory is commonly described by state-and-transition models that summarize ideas about how complex systems work through alternative ecosystem states, feedback loops, thresholds, and triggers (Bagchi et al. 2012; Ratajczak et al. 2014).

Multistate models are an alternative to empirically quantify ecosystem dynamics (Veran et al. 2012; Zweig and Kitchens 2014) by including measurements of states, linear models and maximum likelihood approaches to estimate how environmental covariates influence transition probabilities between states. Breininger et al. (2010) previously used multistate models and multi-model inference to quantify habitat state transition probabilities of potential Florida scrub-jay territories at 5-year intervals (1994-2004) using combinations of environmental factors as covariates. Breininger et al (2010) used landscape units that defined potential Florida scrub-jay territories because transition probabilities within potential territories provide the parameters to predict how alternative management actions can be used to better manage and restore the scrub

and flatwoods ecosystem (Johnson et al. 2011; Williams et al. 2011). Florida scrub-jays are the primary biodiversity management indicator in the scrub and flatwoods ecosystem based on regulatory guidance (Adrian 2006).

Here we use multistate modeling and multi-model inference to predict how annual habitat state transition probabilities (2004-2015) are influenced by environmental covariates important from earlier work (Breininger et al. 2010) in addition to fire history, rainfall, and open sandy areas. Earlier covariates included vegetation type, edges (forests, roads), and management actions (fire, cutting). Other than observations, there has been little work quantifying fire history effects on habitat transitions (Bradstock et al. 2005). Open sandy areas are important habitat components for biodiversity and can influence fire spread (Schmalzer 2003; Menges et al. 2008; Duncan et al. 2015).

METHODS

STUDY SYSTEM

Our study was conducted on Kennedy Space Center/ Merritt Island National Wildlife Refuge (KSC/MINWR), a barrier island complex located along central Florida's Atlantic Coast. Oak scrub and flatwoods are heterogeneous vegetative communities dominated by scrub oaks, saw palmetto, grasses and ericaceous plants. Cover of scrub oaks is greatest on the most well-drained soils ("oak") and declines on moderately drained soils ("flatwoods") where the more flammable flatwoods species increase. Although considered distinct plant communities, oak and flatwoods are often intermixed at a scale where individual fires cross vegetative types and fire management units usually include a mixture of plant communities (Breininger et al. 2002). Plant composition

changes little after fire because most plants are clonal and re-sprout within weeks (Schmalzer and Hinkle 1992).

Scrub and flatwoods on KSC/MINWR had many openings and little forest prior to a fire suppression period (1950-1978), which caused a loss of openings and increases in tall shrubs and forests (Duncan et al. 1999). Many forests were once marshes that are abundant in the scrub and flatwoods ecosystem. A prescribed fire program followed focusing on fuels management as part of a national program to reduce threats of catastrophic fires on human interests. Getting the ecosystem back to native short and medium habitat states has been difficult, as tall shrubs and forests burn poorly and mechanical cutting is generally needed to reintroduce fire into degraded areas (Schmalzer and Boyle 1998). Currently, the fire return interval in a management unit can be as often as 3-5 years, but the average fire cycle is much longer (Duncan et al. 2009).

DATA COLLECTION

Habitat states were determined for all 695 potential Florida scrub-jay territories, delineated as 10-ha square polygons within population core and connecting areas managed by prescribed fires (Carter et al. 2006). Individual fires in oak and flatwoods often burn in mosaic patterns so that potential territories include patches of vegetation with different fire histories.

Shrub height within potential territories provides a rapid approach to classify potential territories into categories (states) useful for describing habitat quality and informing fire management (Breininger et al. 2010; Johnson et al. 2011). We measured habitat states each year from 2004-2015 using 1.0 m resolution photography and field observations (Breininger et al. 2010). Years were defined as April 1 to March 31 corresponding to Florida scrub-jay nesting season and the timing of most aerial photographs. Short habitat has many openings between

shrubs, medium habitat has a uniform (flat) appearance and tall has texture resulting from shade. Short territories lack shrubs > 1.2 m tall and had experienced a recent, extensive burn. Medium territories include at least 0.4 ha of shrubs 1.2-1.7 m tall (optimal height) and exclude large patches (>1.0 ha) of tall shrubs (>1.7 m tall). On average it takes 8 years without disturbance for oaks to reach medium height (Schmalzer and Hinkle 1992; Duncan et al. 1995). Tall territories include areas with > 1.0 ha of tall shrubs and usually include shorter shrubs but few open sandy areas (Breininger et al. 2014b).

Our approach for applying broad habitat states described above does not consider all elements of Florida scrub-jay habitat quality (Burgman et al. 2001), but characterizing landscape units into these states is practical enough to conduct across broad geographic areas while informing habitat management decision making. Short and tall states are population sinks where mortality exceeds recruitment and the preferred medium state is a source where recruitment exceeds mortality, based on 25 years of demographic studies (Breininger et al. 2014b).

We identified a suite of covariates predicted to influence the transition probabilities between habitat states. The static (non-time varying) covariate “oak” identified potential territories intersecting well-drained soils and “flatwoods” identified potential territories that included moderately drained soils with smaller patches of oaks that are found on well-drained soils. The static covariate “edge” recorded whether a man-made, open-water, or forest edge intersected a potential territory as edges impede fire spread. The dynamic (time varying) covariate “open” distinguished whether open sandy areas were in $>50\%$ of the vegetation per territory. The dynamic covariate “cutting” distinguished territories where at least $\frac{1}{4}$ of the territory was subject that year to mechanical cutting of trees and shrubs.

The fire history of territories differed across the KSC/MINWR landscape; in order to encompass these differences we incorporated several dynamic covariates related to the fire histories that we predicted had an influence on transition probabilities. The dynamic covariate “fire” distinguished territories where at least ¼ of the territory burned that year based on remote sensing and fire records (Shao and Duncan 2007). The covariate time since fire, “TSF”, was dynamic and represented the number of years since the last fire beginning with the previous fire interval; this covariate was thus independent of “fire” during the interval because fuels could have varied depending on time since the previous fire. The dynamic covariate longest fire interval, “LFI”, represented the longest period without fire during the previous 20 years, recognizing that fire free intervals that approached 20 years resulted in states resilient to fire (Duncan et al. 1999). The final fire covariate “NF” included the number of fires for the previous 10 years because repeated, short-interval fires can deplete underground biomass (Saha et al. 2010).

The dynamic covariate standardized precipitation index, “SPI”, was obtained for Florida climate divisions 3 from the National Climatic Data Center, Asheville, NC (www.ncdc.noaa.gov/). The SPI describes the observed precipitation over a time period as the number of standard deviations above or below the long-term mean precipitation for that time period (McKee et al. 1993) and has been useful in studying responses in scrub vegetation (Foster et al. 2014, 2015). We used the 12-month SPI for April – March 31 as a measure of drought. The 12 month SPI for March compares the cumulative precipitation from the previous April to the current March to the historic pattern of precipitation for that time period.

DATA ANALYSES

We used multistate models to analyze annual transition probabilities between states (Fig. 1) as a multinomial model of static and dynamic environmental covariates. Static variables were oak/flatwoods and edge/no edge. One dynamic variable (SPI) was the same for all potential territories, but unique to each interval. Other dynamic variables were specific to each interval and potential territory: fire/no fire, mechanical cutting/no cutting, openings/no openings, 3 fire history variables.

Each multistate model consisted of a likelihood combining 3 multinomial models, 1 for each of the 3 states. We estimated transition probabilities for state changes (e.g., short-to-medium); transition probability estimates of states remaining the same between years (e.g., short-to-short) were estimated by subtracting 1.0 minus the transition probability estimates from state changes. The transition of short-to-tall was constrained to zero because it didn't occur, which enhanced numerical estimation. We developed 40 competing models representing hypotheses of how combinations of different variables, two-way interactions, linear and quadratic relationships would affect state transitions. Models were implemented in Program Mark (White et al. 2006), which produced an AIC_c model-selection table, estimates of β s (regression parameters), detection probabilities, and transition probabilities along with and their precision (i.e., SE and CI). We made *a priori* predictions about the direction for each β , similar to the previous modeling (Breininger et al. 2010).

We provided a simple approach to present how state transitions and measures of precision varied annually for oak and flatwoods without environmental covariates because oak and flatwoods are often considered distinct plant communities. We also predicted future abundances of each state for the next 12 years by Markov projections, beginning with the 2015 vector of state abundances. The Markov matrices for the future predictions were estimated with time constant

models, separately for oak and flatwoods without other environmental covariates (Breininger et al. 2010).

RESULTS

Six models had > 99% of the empirical support with similarities regarding covariate effects on transition probabilities (Table 1). The importance of covariates often differed among transition probabilities and included nonlinear effects and interactions, including differences between oak and flatwoods. Models with support included all covariates important (oak, edge, fire, and cutting) from Breininger et al. (2010) and the new covariates involving fire history (time-since-fire, longest fire free interval, number of fires in previous 10 years, openings) and annual rainfall (standardized precipitation index).

We presented only the top model (Table 2) because β 's absent in the top model had numerical estimation errors (i.e. unreasonable standard errors). The main effect for β 's describing oak versus flatwoods often had confidence intervals that overlapped zero, but all supported models included an oak versus flatwood effect, and many other covariates had different effects depending on whether the site was oak or flatwoods. Covariates in the top model usually had the same direction of effects we predicted, except for then number of fires in the previous 10 years.

Tall territories remained the most abundant habitat state (Figure 2), but there was much annual variation among most transition probabilities (Table 3). The Markov process for generating a vector of state abundances from time constant transition probabilities predicted little change in state abundances across the next 12 years instead of a medium state abundance increase.

DISCUSSION

Multistate models provided a unifying modeling framework to empirically quantify the effects of many environmental variables on ecosystem dynamics, by breaking a large landscape into potential territories and developing a longitudinal history of states and environmental covariates. No simple model was found that explained ecosystem dynamics; all models with empirical support included many environmental factors for each transition probability; these effects included interactions and nonlinear relationships, as expected given the complexities of fire effects on habitat (Driscoll et al. 2010).

Edges (roads and forests) that resulted from anthropogenic effects were among the most influential factor across transition probabilities; this made sense because edges disrupt fire flow (Duncan and Schmalzer 2004). Human activities associated with habitat fragmentation increase ignitions and fire spread in many other ecosystems, but still have detrimental impacts (Kraaij et al. 2013). Cutting was an important management action influencing transitions as was found in earlier studies (Breininger et al. 2010). This has important management implications, because cutting along edges and frequent fire appear to be the only solution to Florida scrub-jay population recovery on KSC/MINWR (Johnson et al. 2011). However, we agree with colleagues that mechanical cutting is not a replacement for fire and care is needed to avoid the spread of exotics and reducing the cover of species important for spreading fires (Schmalzer and Boyle 1998; Menges and Gordon 2010).

Fire history effects were practical to study in our system because fires in most grid cells generally occurred every few years and not every few decades, or longer. The presence/absence of fire during an annual interval usually had a larger effect than fire history variables, except that TSF had a great effect for the short-to-medium transition in oak. The presence/absence of fire

might have had a lesser impact than TSF because the short generally lacks fuels to burn extensively. The TSF nonlinear effect could be explained by growth being most rapid a few years after fire (Schmalzer and Hinkle 1992). The length of the fire free interval was probably important because scrub accumulates biomass underground and eventually develops a fuels distribution that reduces fire spread (Maliakal et al. 2000; Boughton et al. 2006). The number of fires (NF) did not increase tall-to-short and tall-to medium transitions as we predicted, but the effect was poorly estimated (CI overlapped zero, standard error larger than the mean). The mean effect of NF provides support to some Florida fire managers beliefs that it takes at least 3-5 years for fuels to accumulate enough to carry fires, and that scrub burned too early doesn't accumulate enough fuel to burn hot enough to ignite tall. Other transitions might not have been effected by NSF, as we predicted, because fires didn't burn often enough to deplete underground biomass.

We suspect seasonality could influence system dynamics as most fire effects studied were associated with prescribed fires that differ from the seasonality and meteorology of natural, lightning ignited fires (Duncan et al. 2009). There are many vegetative differences in the flammability within landscapes and grasses are especially important for spreading fire (Breininger et al. 2002). The growth and flowering of many important grass species (e.g., *Aristida stricta*) is dependent on fires that occur at the transition between the dry and thunderstorm seasons when most lightning fires occurred (Platt et al. 1988; Noss 2013). Thus, fire frequency and spread probably changed historically because of anthropogenic effects.

The Pre-European landscape might have been resilient to change because frequent lightning fires could spread easily through grasses among short and medium territories lacking roads and forest edges (Duncan et al. 1999). Early landscapes had many open sandy areas, which usually disappear within 1-2 years after fire in recent times (Schmalzer and Hinkle 1992). The negative

relationship we observed between the amount of openings and the transition from medium-to-tall might have occurred because the areas with lots of openings were indicators of slower growth. Slower growth might have resulted from site differences (e.g., topography) or fire severity. We are investigating methods to develop longitudinal fire severity histories across our study sites because we recognize severity could also be an important covariate (Lindenmayer et al. 2013; Fang et al. 2015).

Anthropogenic effects often produce alternative states that are resistant to change (Scheffer and Carpenter 2003; Johnstone et al. 2016). Following 28 years of fire suppression, 35 years of prescribed fires only reduced slightly the extent of tall territories that were resistant to restoration. Other complications included restrictions on prescribed fires that must be ignited under particular wind directions to avoid smoke impacts to smoke sensitive areas. These restoration challenges occur across the geographic region making many small Florida scrub-jay populations vulnerable to extinction (Duncan et al. 2004; Breininger et al. 2006).

Funding for prescribed fires often focuses on maximizing fuels reduction allowing fuels to accumulate until fires can burn them extensively. This causes most potential Florida scrub-jay territories to have too little optimal habitat and thus declining population sizes (Breininger et al. 1999). We believe “optimal habitat management” might be better at reducing catastrophic fire risk than fuels management (Breininger et al. 2014a). In an optimal habitat management strategy, prescribed fires would be initiated sooner than a fuels reduction strategy by attempting prescribed fires before all fuels are likely to ignite thus creating transitory openings and heterogeneity among shrub patches at the territory scale. In habitat occupied by Florida scrub-jays near carrying capacity, optimal habitat management would attempt mosaic fires to provide some unburned patches to serve as nest sites, provide acorns, and areas to escape predators. Such

fire mosaics would require greater post-fire monitoring because unburned patches might reignite. However, fire modeling suggests this strategy would reduce fuels continuity decreasing the risk of spreading potentially catastrophic fires (e.g., wildfires) that are expensive to control (Duncan et al. 2015) .

Our study does not take into account the effects of a changing climate; however, it is likely that the areal extent of oak and flatwoods will be reduced with rising sea levels putting pressure on managing biodiversity in increasingly smaller areas. Changes in precipitation might include heavier precipitation events and longer periods between precipitation events; droughts may become more frequent (Karl et al. 2009). We observed the effects of SPI on oak transitions to earlier successional states were not linear because drought promotes fire spread, but extreme droughts force a shutdown of prescribed fire because of increased catastrophic fire risk. Droughts might not have effected flatwoods because the vegetation is more flammable and the water table closer to the root zone (Schmalzer and Hinkle 1992).

Scientists need to broaden study implications, but generalizations also lead to debates as to whether Florida scrub-jays, for example, should be a scrub management indicator for all scrub (Menges and Gordon 2010). A nuanced approach may need to consider regional biodiversity where opportunities for conservation vary among species and conservation areas. In our study region, conservation opportunities are greatly limited by urbanization and differences occur in the geographic range of species (Duncan et al. 2004). Most species of conservation concern in our study site benefited by conditions best for Florida scrub-jays, and we know of no species of conservation concern that would decline from Florida scrub-jay management directed at one of the species last remaining extant large populations.

Plant ecologists recommend pyrodiversity to account for the requirements of lesser known species while animal ecologists have increasingly challenged whether pyrodiversity creates faunal biodiversity (Parr and Andersen 2006; Menges 2007; Clarke 2008; Farnsworth et al. 2014). Our study site had great pyrodiversity but shifted to being poor habitat quality for Florida scrub-jays. Rather than simple statistical distributions, fire frequency should be based on species biology (Gill and McCarthy 1998; Kelly et al. 2015), such as habitat and population state (Johnson et al. 2011; Williams et al. 2011).

Long-term studies have shown differences in geographic responses to fire between study sites and fire return rates (Menges et al. 2008). Depth to water table, nutrient availability, and the geological age of soils help explain geographic differences in vegetative responses to fire (Schmalzer and Hinkle 1992). Broad scale approaches often do not consider spatio-temporal complexities and fine scale habitat features important to endemic species (Bond and Parr 2010; Watson et al. 2011; Noss et al. 2015). We believe our study strength is demonstrating a monitoring approach to evaluate how management and environmental factors interact to effect habitat quality while being site-specific.

Monitoring is often most effective when it informs decision making (Nichols and Williams 2006). The transition probabilities estimated herein can be updated through monitoring to drive management decision models (Johnson et al. 2011; Williams et al. 2011) and link habitat quality to population predictions (McCarthy and Thompson 2001; Akcakaya et al. 2004; Burgman et al. 2005; Duarte et al. 2016). Multistate modeling enhanced the ability to examine relationships among environmental factors and fire history, as such relationships have been understudied (Haslem et al. 2012; Levick et al. 2015).

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Table 1. Model selection table for top 6 models (AICc weight > 0.01)^a.

Table 2. Comparing regression slopes (β 's) with *a priori* predictions for the best habitat transition model.

Table 3. Annual transition probability estimates (95% CI)

Model	Transition probabilities (ψ) and covariates that differed among the top models						Model selection results			
	Longest fire interval	SPI \times Fire	Openings	Openings \times Oak	Number fires	Number fires \times Oak	Delta AICc	AICc Weight	No. parameters	Deviance
1	$\psi^{SM} \psi^{TS} \psi^{TM}$		ψ^{MT}		$\psi^{TS} \psi^{TM}$		0.00	0.44	45	4420
2	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		ψ^{SM}	ψ^{MS}		$\psi^{TS} \psi^{TM}$	1.39	0.22	50	4411
3	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		ψ^{MT}				1.67	0.19	42	4427
4	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		$\psi^{SM} \psi^{MT}$	ψ^{MS}			3.72	0.07	48	4417
5	$\psi^{SM} \psi^{TS} \psi^{TM}$	$\psi^{MS} \psi^{TS} \psi^{TM}$	ψ^{MT}		$\psi^{TS} \psi^{TM}$		5.19	0.03	55	4405
6	$\psi^{SM} \psi^{MS} \psi^{TS} \psi^{TM}$		$\psi^{SM} \psi^{MT}$		$\psi^{TS} \psi^{TM}$		5.25	0.03	52	4411

^a Superscripts refer to particular transition probabilities between states ^S = short, ^M = medium, ^T = tall. All top models included the effects of edge and oak \times fire for all ψ . All top models included a quadratic relationship for effect of time since fire (TSF) \times oak for ψ^{SM} . All top models included a linear TSF effect for ψ^{MT} . The effect of SPI (standardized precipitation index) applied only to oak for ψ^{MS} , ψ^{TS} , ψ^{TM} among the top models. The effect of cutting applied only to ψ^{MT} , ψ^{TS} , and ψ^{TM} for top models.

Transitions (ψ)	β description	β	Lower CL	Upper CL	<i>A priori</i> prediction	Explanation
ψ^{SM}	Flatwoods vs oak	-1.12	-1.93	-0.32	-	Agreement, flatwoods more likely to burn extensively
ψ^{SM}	Edge	0.41	0.12	0.70	+	Agreement, edges reduce fire spread
$\psi^{SM \text{ oak}}$	Fire vs no fire	-0.11	-0.77	0.56	-	Agreement, fires reduce height
$\psi^{SM \text{ flatwoods}}$	Fire vs no fire	-1.56	-2.36	-0.76	-	Agreement, fires reduce height
$\psi^{SM \text{ oak}}$	TSF	0.48	0.26	0.70	+	Agreement, growth after fire
$\psi^{SM \text{ oak}}$	TSF squared	-0.02	-0.03	-0.01	-	Agreement, growth rapid immediately after fire than slows
$\psi^{SM \text{ flatwoods}}$	TSF	1.01	0.66	1.36	+	Agreement, growth after fire
$\psi^{SM \text{ flatwoods}}$	TSF squared	-0.08	-0.12	-0.05	-	Agreement, growth rapid immediately after fire than slows
ψ^{SM}	LFI	0.04	0.01	0.07	+	Agreement, longer fire intervals allow faster regrowth
ψ^{MS}	Flatwoods vs oak	0.05	-1.04	1.14	+	Ambiguous, we predicted flatwoods more likely to burn extensively
ψ^{MSoak}	Edge	-0.78	-1.22	-0.35	-	Agreement, edges reduce fire spread
ψ^{MSoak}	Fire vs no fire	3.38	2.51	4.24	+	Agreement, fires reduce height
$\psi^{MSflatwoods}$	Fire vs no fire	3.72	2.96	4.49	+	Agreement, fires reduce height
ψ^{MSoak}	SPI	-1.17	-1.79	-0.54	-	Agreement, fire spread increases in drought for oak

ψ^{MSoak}	SPI squared	-1.49	-2.04	-0.95	-	Agreement, no prescribed fire in extreme drought
ψ^{MT}	Flatwoods vs oak	0.06	-0.27	0.39	+	Ambiguous, we predicted flatwoods recovers faster than oak
ψ^{MT}	Edge	1.07	0.74	1.39	+	Agreement, edges reduce fire spread
$\psi^{MT\ oak}$	Fire vs no fire	-0.58	-1.11	-0.05	-	Agreement, fires reduce height
$\psi^{MT\ flatwoods}$	Fire vs no fire	-0.24	-0.80	0.31	-	Agreement, fires reduce height
ψ^{MT}	TSF	0.06	0.01	0.11	+	Agreement, growth after fire
ψ^{MT}	Cutting	-2.09	-4.07	-0.11	+	Agreement, mechanical cutting decreases height
$\psi^{MT\ oak}$	Openings	-1.46	-1.94	-0.97	+ and -	Clarification, open areas are a sign of slower recovery
ψ^{TS}	Flatwoods vs oak	0.91	-0.49	2.30	+	Agreement, we predicted flatwoods more likely to burn extensively
$\psi^{TS\ oak}$	Edge	-1.36	-1.83	-0.90	-	Agreement, edges reduce fire spread
$\psi^{TS\ oak}$	Fire vs no fire	3.94	2.67	5.22	+	Agreement, fires reduce height
$\psi^{TS\ flatwoods}$	Fire vs no fire	3.42	2.73	4.11	+	Agreement, fires reduce height
$\psi^{TS\ oak}$	Cutting	2.19	1.63	2.75	+	Agreement, mechanical cutting decreases height
$\psi^{TS\ oak}$	SPI	-1.07	-1.89	-0.25	-	Agreement, fires increase in drought
$\psi^{TS\ oak}$	SPI squared	-1.12	-1.72	-0.51	-	Agreement, no prescribed fire in extreme drought
ψ^{TS}	Number fires	-0.17	-0.43	0.09	-	Disagreement, we predicted more fires increase recovery

ψ^{TS}	LFI	-0.03	-0.07	0.01	-	Agreement, longer fire intervals slow restoration to earlier states
ψ^{TM}	Flatwoods vs oak	1.50	-0.21	3.21	+	Agreement, we predicted flatwoods more likely to burn extensively
$\psi^{\text{TM oak}}$	Edge	-0.71	-1.21	-0.21	-	Agreement, edges reduce fire spread
$\psi^{\text{TM oak}}$	Fire vs no fire	4.50	3.08	5.92	+	Agreement, fires reduce height
$\psi^{\text{TM flatwoods}}$	Fire vs no fire	3.48	2.55	4.42	+	Agreement, fires reduce height
ψ^{TM}	Number fires	-0.25	-0.51	0.01	-	Disagreement, we predicted more fires increase recovery
ψ^{TM}	LFI	-0.09	-0.13	-0.04	-	Agreement, longer fire intervals slow restoration to earlier states
ψ^{TM}	Cutting	0.62	-0.08	1.32	+	Agreement, mechanical cutting decreases height
$\psi^{\text{TM oak}}$	SPI	-0.87	-1.54	-0.20	-	Agreement, fires increase in drought
$\psi^{\text{TM oak}}$	SPI squared	-0.01	-0.52	0.50	-	Agreement, droughts have biggest effect

Transition probability superscripts were SM for short to medium, MS for medium to short, MT for short to tall, TS for tall to short, TM for tall to medium. Superscripts that included oak had a β specific to oak, superscripts that included flatwoods had a β specific to flatwoods and superscripts without oak or flatwoods had one β for both oak and flatwoods transitions. Abbreviations TSF = Time-since-fire, LFI = longest fire interval, SPI = standardized precipitation index. Nonlinear relationships were represented by a squared term (quadratic).

year	short-medium	medium-short	medium-tall	tall-short	tall-medium
scrub					
2004-2005	0.57(0.45-0.68)	n/a	0.18(0.12-0.26)	0.00(0.00-0.03)	0.01(0-0.04)
2005-2006	0.71(0.53-0.84)	0.04(0.02-0.09)	0.29(0.22-0.37)	0.01(0.00-0.04)	n/a
2006-2007	0.22(0.09-0.46)	n/a	0.09(0.05-0.16)	0.00(0.00-0.03)	0.01(0.01-0.04)
2007-2008	0.40(0.19-0.65)	0.28(0.21-0.37)	0.03(0.01-0.08)	0.08(0.05-0.11)	0.03(0.01-0.05)
2008-2009	0.19(0.11-0.31)	0.02(0.01-0.08)	0.05(0.02-0.12)	0.01(0-0.03)	0.03(0.01-0.06)
2009-2010	0.13(0.06-0.25)	0.01(0.00-0.07)	0.04(0.01-0.1)	n/a	n/a
2010-2011	0.48(0.34-0.62)	0.05(0.02-0.11)	0.15(0.09-0.23)	0.04(0.02-0.08)	0.03(0.02-0.06)
2011-2012	0.46(0.32-0.61)	0.06(0.03-0.12)	0.07(0.03-0.13)	0.03(0.02-0.06)	0.14(0.11-0.19)
2012-2013	0.24(0.13-0.41)	0.08(0.05-0.14)	0.02(0.01-0.06)	n/a	0.00(0.00-0.03)
2013-2014	0.12(0.05-0.26)	n/a	0.02(0.01-0.06)	n/a	n/a
2014-2015	0.17(0.08-0.32)	0.01(0.00-0.05)	0.07(0.04-0.12)	n/a	0.01(0-0.04)
flatwoods					
2004-2005	0.54(0.66-0.54)	0.09(0.04-0.20)	0.31(0.21-0.45)	0.08(0.05-0.13)	0.01(0-0.05)

2005-2006	0.38(0.26-0.52)	0.10(0.05-0.19)	0.31(0.21-0.42)	0.01(0.00-0.04)	n/a
2006-2007	0.23(0.12-0.39)	0.05(0.02-0.14)	0.21(0.13-0.33)	0.03(0.01-0.06)	n/a
2007-2008	0.16(0.07-0.31)	0.16(0.09-0.29)	0.11(0.05-0.22)	0.07(0.04-0.12)	0.01(0.00-0.04)
2008-2009	0.15(0.07-0.26)	0.15(0.07-0.28)	0.06(0.02-0.18)	0.03(0.01-0.06)	0.04(0.02-0.08)
2009-2010	0.12(0.06-0.23)	n/a	0.02(0.00-0.12)	n/a	n/a
2010-2011	0.44(0.31-0.58)	0.02(0.00-0.11)	0.12(0.06-0.23)	0.01(0.00-0.04)	0.01(0.00-0.04)
2011-2012	0.25(0.13-0.43)	0.17(0.10-0.28)	0.03(0.01-0.1)	0.12(0.08-0.18)	0.10(0.06-0.15)
2012-2013	0.10(0.05-0.21)	0.22(0.15-0.32)	0.01(0.00-0.08)	0.04(0.02-0.09)	0.07(0.04-0.12)
2013-2014	0.08(0.03-0.16)	n/a	0.07(0.03-0.15)	n/a	n/a
2014-2015	0.25(0.16-0.36)	0.11(0.06-0.2)	0.11(0.06-0.20)	0.08(0.05-0.14)	0.07(0.04-0.13)

n/a = annual transitions that did not occur

Figure 1. Habitat quality states and transition probabilities (ψ) where superscripts sequentially indicate transitions between particular states.

Figure 2. Annual habitat state abundances for (a) scrub, (b) flatwoods.



